GENERAL NOTES

Respiratory gas concentrations and temperatures within the burrows of three species of burrow-nesting birds.—Many species of birds nest in underground burrows. Occupants of such nests are generally protected from both predators and adverse weather conditions (Hoogland and Sherman, Ecol. Monogr. 46:33–58, 1976). However, respiratory gas concentrations within burrows may be significantly different from normal atmospheric values or those in open nests (Walsberg, Am. Zool. 20:363–372, 1980). In the burrows of the four species studied to date, oxygen and carbon dioxide concentrations are lower and higher, respectively, than normal atmospheric levels (White et al., Physiol. Zool. 51:140–154, 1978; Ackerman et al., Physiol. Zool. 53:210–221, 1980; Wickler and Marsh, Physiol. Zool. 54: 132–136, 1981; Pettit et al., Physiol. Zool. 55:162–170, 1982). The levels of carbon dioxide and oxygen encountered in burrows are known to have pronounced physiological effects on birds (Scheid, pp. 405–453 *in* Avian Biology, Vol. 6, Farner et al., eds., Academic Press, New York, New York, 1982), hence they are of particular interest. In this note we report on respiratory gas concentrations and temperatures within the burrows occupied by Rhinoceros Auklets (*Cerorhinca monocerata*), Burrowing Owls (*Athene cunicularia*), and Bank Swallows (*Riparia riparia*).

Methods.—Air temperatures and gas concentrations were measured in 26 burrows occupied by Bank Swallows in Missoula, Missoula Co., Montana during 1978, in six burrows occupied by Burrowing Owls in Payette County, Idaho, in 1980 and 1981, and in seven burrows occupied by Rhinoceros Auklets on Protection Island, Kitsap Co., Washington, in 1980. At each of these localities gas concentrations were also measured in burrows previously used by these species but unoccupied at the time.

Burrow temperatures were measured with thermistor probes (Yellow Springs Instruments) individually calibrated with a National Bureau of Standards certified thermometer. Reported temperatures are accurate within ±0.1°C.

Gas samples were withdrawn from burrows through flexible tubing (1–6 mm ID) inserted into the burrow. A volume 1.5–4 times that of the sample tube was withdrawn from the burrow and vented to the atmosphere immediately before the gas sample to be analyzed was taken. The total volume of air withdrawn from any burrow was less than 3% of the estimated burrow volume. Samples of air from Bank Swallow burrows were drawn into gas-tight 2.5-cm³ glass syringes, sealed, and either immediately analyzed or transported to the lab for analysis. Equilibration of burrow gas samples in the syringes with the atmosphere was minimal as determined by experiments with certified gas standards. Carbon dioxide and oxygen concentrations in these samples were determined with a 0.5-cm³ Scholander micro-gas analyzer (Scholander, J. Biol. Chem. 167:235–250, 1947). Fyrite oxygen and carbon dioxide analyzers with sample volumes of 0.5 l were used to analyze air samples from the burrows occupied by auklets and owls. The Fyrite analyzers were calibrated with gas standards whose accuracy was checked with the Scholander analyzer. Gas concentrations are accurate within ±0.05 volume percent.

The position of the temperature probes and gas sampling tubes within burrows and number and relative age of burrow occupants was confirmed by visual inspection or by excavation except in five burrows occupied by Burrowing Owls. The location and depth of these latter burrows, in addition to the nature of the soil in which they were sited, precluded their excavation.

Results and discussion.—Mean air temperatures in the burrows of these three species are

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markedly different, ranging from 18.0–29.1°C (Table 1). These species differences are statistically significant ($P < 0.05$). The air temperatures within Bank Swallow burrows that are reported here are within the ranges of those previously reported (e.g., Stoner, Roosevelt Wild Life Annals 4:126–233, 1936; Ellis, Condor 84:441–443, 1982), however, the air temperatures in burrows occupied by Burrowing Owls and Rhinoceros Auklets are lower than those measured by Coulombe (Condor 73:162–176, 1971) and Richardson (Condor 53:456–473, 1961), respectively. These differences and similarities in mean air temperatures within burrows undoubtedly reflect similarities and differences in geographic location of burrows and when these measurements were made. The relatively narrow range of air temperatures (3–5°C) observed in those burrows occupied by individuals of the same species (Table 1) are indicative of the equability of the thermal microenvironment of burrows.

The mean respiratory gas concentrations in the air of burrows occupied by Rhinoceros Auklets, Burrowing Owls, and Bank Swallows are significantly different ($P < 0.05$) from those in atmospheric air (20.95% oxygen and 0.03% carbon dioxide) (Gilbert, pp. 153–176 *in* Handbook of Physiology, Respiration, Vol. 1, Fenn and Rahn, eds., American Physiological Society, Washington, D.C., 1964) and in the air of unoccupied burrows (Table 1). The oxygen and carbon dioxide concentrations in occupied Bank Swallow burrows are the most extreme of the three species studied and are statistically different at the 95% probability level from the gas concentrations in the burrows of the other two species. The mean oxygen and carbon dioxide concentrations in occupied Bank Swallow burrows are nearly 2 volume % less and more, respectively, than those, for example, in burrows occupied by auklets. Gas concentrations in the burrows occupied by Burrowing Owls are intermediate to those in occupied auklet and swallow burrows. A similar range of variation in burrow gas environments is also apparent when data available for other species' burrows are examined (Table 2). As is apparent in Table 2, burrow gas environments are either very near that of the free atmosphere or deviate considerably from atmospheric values. These variations in the composition of gas environments in burrows occupied by different species may result from differences in gas sampling or measuring techniques, but more probably result from differences in number and size of occupants, variations in soil air composition, and adequacy of burrow gas exchange or ventilation.

Despite the differences in techniques used to sample and measure respiratory gas concentrations in burrows (see Table 2 for references) the only likely source of error of this type that might yield variation of the order observed in Tables 1 and 2 concerns where air samples were collected relative to the position of the burrow occupants. Only in burrows occupied by Burrowing Owls was the proximity of the sampling tube to the occupants not assessable. Burrowing Owls were occupying abandoned badger (*Taxidea taxus*) burrows, where the nest tends to be in a side chamber off the main tunnel. Because there is a gradient in respiratory gas concentrations as one moves away from burrow inhabitants (Wilson and Kilgore, J. Theoret. Biol. 71:73–101, 1978) this architectural arrangement would usually result in samples being taken outside the nest chamber and consequently in gas concentrations lower than the real maximum for carbon dioxide and higher than the real minimum for oxygen.

Variation in the relationship between total mass of burrow occupants and nest-chamber volume probably explains much of the variation in burrow gas concentrations observed in Tables 1 and 2 (Wilson and Kilgore, 1978). The occupied Bank Swallow burrows we studied contained from 2–6 young of varying ages and in most instances usually contained an adult. In these burrows, there is a significant ($P < 0.05$) positive correlation ($r = 0.88$) between carbon dioxide concentration in burrow air and number of occupants (and therefore mass) and a significant ($P < 0.05$) negative correlation ($r = -0.89$) between oxygen concentration and number of occupants. Similar findings have been reported by Wickler and Marsh (1981). The most extreme oxygen and carbon dioxide environments in burrows of this species occur in those with 4–6 young of near fledging size where the mass to volume ratio is 0.4–0.8 g·

TABLE 1

TEMPERATURES AND RESPIRATORY GAS CONCENTRATIONS WITHIN THE BURROWS OF THREE SPECIES OF BURROW-NESTING BIRDS

Species	% oxygen			% carbon dioxide			Temperature (°C)		
	N[a]	$\bar{x} \pm SE$	Range	N	$\bar{x} \pm SE$	Range	N	$\bar{x} \pm SE$	Range
Rhinoceros Auklet									
(Cerorhinca monocerata)									
occupied (7)[b]	11	19.0 ± 0.2	17.0–19.8	9	1.1 ± 0.1	0.7–1.6	9	18.0 ± 0.5[d]	16.0–20.5
unoccupied (9)	8	20.3 ± 0.2[c]	19.0–20.9	5	0.6 ± 0.1[c,d]	0.3–1.0		—	—
Burrowing Owl									
(Athene cunicularia)									
occupied (6)	6	19.7 ± 0.2	18.9–20.3	6	1.7 ± 0.3	0.5–2.8	9	20.1 ± 0.6[d]	17.7–22.9
unoccupied (5)	3	21.0 ± 0.0[c]	21.0–21.0	5	0.2 ± 0.1[c,d]	0.0–0.5		—	—
Bank Swallow									
(Riparia riparia)									
occupied (26)	56	17.4 ± 0.3[e]	13.2–20.8	58	3.1 ± 0.2[e]	0.4–6.7	42	29.1 ± 0.1[d]	27.6–30.8
unoccupied (3)	7	20.6 ± 0.1[c]	20.3–21.0	7	0.4 ± 0.0[c,d]	0.2–0.5		—	—

[a] Number of observations.
[b] Number of burrows in parentheses.
[c] Statistically different from occupied, t-test, $P < 0.05$ (ts = 3.69, 2.22, 9.75, 3.05, 4.39, 11.36).
[d] Statistically different from atmospheric air (see text), t-test, $0.001 < P < 0.05$ (ts = 6.52, 3.69, 31.01).
[e] Statistically different from other species, F-test and Least Significant Difference test, $P < 0.05$ (Fs = 5.920, 7.230).

TABLE 2
SUMMARY OF RESPIRATORY GAS CONCENTRATIONS WITHIN BIRD BURROWS

Species	Nᵃ	% oxygen		% carbon dioxide		Reference
		$\bar{x}$	Minimum	$\bar{x}$	Maximum	
Wedge-tailed Shearwater (*Puffinus pacificus*)	12	19.6[b]	—	0.1[b]	—	Ackerman et al. 1980
Bonin Petrel (*Pterodroma hypoleuca*)	18	19.8[b]	—	0.7[b]	—	Pettit et al. 1982
Rhinoceros Auklet (*Cerorhinca monocerata*)	7	19.0	17.0	1.1	1.6	Present study
Burrowing Owl (*Athene cunicularia*)	6	19.7	18.9	1.7	2.8	Present study
European Bee-eater (*Merops apiaster*)	20	18.2[c]	15.2[c]	3.3	6.5	White et al. 1978
Bank Swallow (*Riparia riparia*)	34	17.8	14.6	2.6	5.6	Wickler and Marsh 1981
	26	17.4	13.2	3.1	6.7	Present study

[a] Number of burrows.
[b] Assumes a barometric pressure of 760 torr.
[c] Assumes that atmospheric air contains 20.95% oxygen.

cm^{-3}. Nest chamber volume was calculated from actual burrow dimensions assuming an ellipsoidal configuration of the nest chamber and mass of fledglings was assumed to be similar to that measured by Marsh (Physiol. Zool. 52:340–353, 1979). In contrast, the extensive nest chambers of auklet burrows (up to 9.3 l) were occupied by single chicks, 1–9 days of age; one burrow also contained an adult. The near atmospheric respiratory gas concentrations in auklet burrows, as well as those of Bonin Petrels (Pettit et al. 1982) and Wedge-tailed Shearwaters (Ackerman et al. 1980) may therefore reflect this small mass to volume ratio (mean of 0.4 $g \cdot cm^{-3}$). Mass to volume ratios were calculated from burrow dimensions and nestling masses reported by Richardson (1961).

The slopes of the relationships between increase in carbon dioxide ($\Delta\%CO_2 = \%CO_2$ in burrow $- 0.03$) and decrease in oxygen concentrations ($\Delta\%O_2 = 20.95 - \%O_2$ in burrow) in occupied burrows are indicators of the use, production, and exchange of respiratory gases within burrows. These relationships in the burrows of the three species we studied are as follows:

Rhinoceros Auklets

$$\Delta\%CO_2 = 0.86 + 0.11\Delta\%O_2 \ (N = 9; \ s_{y.x} = 0.08)$$

Burrowing Owls

$$\Delta\%CO_2 = 0.07 + 1.20\Delta\%O_2 \ (N = 6; \ s_{y.x} = 0.20)$$

Bank Swallows

$$\Delta\%CO_2 = 0.11 + 0.84\Delta\%O_2 \ (N = 55; \ s_{y.x} = 0.07)$$

Slopes that exceed the respiratory exchange ratio (carbon dioxide production/oxygen consumption) of the occupants (approximately 0.8; see Wickler and Marsh 1981) suggest that there are either additional sources for the carbon dioxide in the air of these occupied burrows, most likely from the soil, or that there is significant non-convective (i.e., diffusive) exchange of gases in these burrows. Slopes at 0.8 suggest that convective exchange (bulk flow) is the most important determinant of burrow gas composition since bulk flow of air into and out of the burrow should not alter the carbon dioxide/oxygen ratio. If the slope is less than the respiratory exchange ratio then non-convective exchange of carbon dioxide favors its loss from the burrow. The slopes of the above relationships in auklets and owls are statistically different (auklets, $t = 8.62$, $P < 0.01$; owls, $t = 2.98$, $P < 0.01$) from 0.8; however, the slope of this relationship in burrows occupied by Bank Swallows is not. Wickler and Marsh (1981) also reported a carbon dioxide to oxygen ratio of 0.86 in occupied burrows of Bank Swallows.

The relatively low levels of carbon dioxide in the burrows of Rhinoceros Auklets suggest that bulk flow of gases into and out of burrows of this species resulting from changes in barometric pressure, thermal differences between the burrow and atmospheric air, movements of occupants back and forth in the burrow acting as pistons, surface winds or passive ventilation are not relatively important, a conclusion supported by observations in Bonin Petrel burrows (Pettit et al. 1982). Presumably then, diffusive gas exchange is the primary means of burrow ventilation in these birds. Auklets, shearwaters, and petrels all construct relatively long burrows (up to 3 m); however, nest chambers in these burrows are usually within 0.5 m of the soil surface (Richardson 1961, Ackerman et al. 1980, Pettit et al. 1982). Also, the moist sandy soils in which these burrows are excavated would presumably promote the differential loss or absorption of carbon dioxide from the burrow atmosphere (Withers, Am. Nat. 112:1101–1112, 1978; Wilson and Kilgore 1978).

The accumulation of carbon dioxide in burrows occupied by Burrowing Owls as indicated by the slope of the relationship between increment in carbon dioxide and decrement in oxygen in burrows, especially considering the low levels of carbon dioxide in burrows

unoccupied by this species (Table 1), would seemingly indicate that diffusive losses of carbon dioxide from these burrows to the atmosphere are reduced.

In the burrows occupied by Bank Swallows convective means of ventilation appear to play a major role in determining the burrow gas environment. Evidence in support of this conclusion, in addition to the magnitude of the slope in the above relationship relating increases in carbon dioxide to decreases in oxygen in burrows of this species, comes from data relating burrow gas concentrations and depth of burrows. There is a positive but non-significant ($P > 0.05$) correlation ($r = 0.29$) between burrow depth and carbon dioxide concentration and a negative but non-significant ($P > 0.05$) correlation ($r = -0.26$) between depth and oxygen concentration in the burrows occupied by Bank Swallows. The same sort of relationships between gas concentration and burrow depth have been reported previously (Wickler and Marsh 1981). Interestingly, convective forms of ventilation have also been shown to be important in the burrows of the European Bee-eater (White et al. 1978).

Our data provide further evidence that the occupants of avian burrows produce and are subjected to respiratory gas environments much different from those in the free atmosphere, while the thermal regime is much buffered from that outside the burrow. The respiratory gas environments to which burrow-nesting birds are exposed are quite similar to those measured in many mammal burrows (for a review of the literature see Arieli, Comp. Biochem. Physiol. 63A:569–575, 1979; Maclean, Comp. Biochem. Physiol. 69A:373–380, 1981). Many of these fossorial mammals show a variety of physiological adjustments that help them cope with life-long exposure to low oxygen, high carbon dioxide environments (e.g., Darden, J. Comp. Physiol. 78:121–137, 1972; Ar et al., Respir. Physiol. 30:201–218, 1977; Arieli and Ar, J. Appl. Physiol. 47:1011–1017, 1979). Recent studies have revealed similar physiological adaptations in burrow dwelling birds as well (Kilgore and Birchard, Am. Zool. 20:766, 1980; Birchard and Kilgore, Physiol. Zool. 53:284–292, 1981; Boggs and Kilgore, J. Comp. Physiol. 149:527–533, 1983; Boggs et al., Comp. Biochem. Physiol. 77A:1–7, 1984).

Sexual differences in longevity of House Sparrows at Calgary, Alberta. — The extensive body of data on survivorship of House Sparrows (*Passer domesticus*) obtained by Summers-Smith (The House Sparrow, Collins, London, England, 1963) and available from British and North American banding studies has been summarized by Dyer et al. (pp. 55–103 *in* Granivorous Birds in Ecosystems, J. Pinowski and S. C. Kendeigh, eds., Cambridge Univ. Press, Cambridge, England, 1977). In England, about 19% of House Sparrow fledglings survive to 1 year post-fledging, and annual adult survival from 1 year onward is about 50% in England and 34% in North America. Female House Sparrows have slightly higher annual survivorship than adult male House Sparrows (51% vs 45%, England; 37.3% vs 32.5%, North America; Dyer et al. 1977). Summers-Smith (1963) found that female mortality was higher than male mortality during the breeding season but the reverse obtained outside the